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Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges

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Scaling laws that describe complex interactions between organisms and their environment as a function of body size offer exciting potential for synthesis in biology^{1–4}. Home range size, or the area used by individual organisms, is a critical ecological variable that integrates behaviour, physiology and population density and strongly depends on organism size^{5–7}. Here we present a new model of home range–body size scaling based on fractal resource distributions, in which resource encounter rates are a function of body size. The model predicts no universally constant scaling exponent for home range, but defines a possible range of values set by geometric limits to resource density and distribution. The model unifies apparently conflicting earlier results and explains differences in scaling exponents among herbivorous and carnivorous mammals and birds^{5–18}. We apply the model to predict that home range increases with habitat fragmentation, and that the home ranges of larger species should be much more sensitive to habitat fragmentation than those of smaller species.

Scaling relationships quantify the universal properties of complex physical and biological systems¹. These relationships can help identify patterns across different levels of biological organization, such as cells, individuals, populations and communities. For example, physiological characteristics of organisms, Y , often vary with body size, M , according to power functions of the general form:

$$Y = Y_0 M^b \quad (1)$$

where b is a scaling exponent, and Y_0 is a taxon- and character-specific normalization constant^{2–4}. Many important physiological rates seem to exhibit constant exponents b that are multiples of $1/4$, which have been recently explained from the fractal branching architecture of organisms⁴. The challenge is to find body size scaling laws and their explanations for interactions between individuals and their environments¹⁹.

Home range, the area used by an animal in its daily and seasonal movements, integrates organism physiology, morphology and behaviour to determine patterns of space use, population density and interactions with other species^{5–7}. As a result, land managers and conservation biologists frequently use home range–body size scaling relationships to determine minimum reserve size and evaluate extinction risks of species⁸. Early studies proposed, and found in preliminary data, that if home range size is directly proportional to resource needs, then $b \cong 3/4$ (refs 9–11). Later studies^{12–14} with more data, however, found that, for all trophic groups combined, $b \cong 1$ and explained deviation in b from $3/4$ *post hoc* as resulting from larger animals encountering a lower resource density and thus causing home range to scale more steeply with size than expected from resource requirements¹⁵. An alternative explanation proposed that home range overlap was greater at larger body sizes, thus reducing resource availability per individual and increasing home range size above that expected from requirements^{5,16}. However, no specific mechanism was proposed for why resource density should be lower or home ranges overlap more for larger species. Lindstedt *et al.*¹⁷ argued that home range should be

proportional to metabolic requirements, which scale as $M^{3/4}$, multiplied by biological time, which scales as $M^{1/4}$, so home range should scale as M^1 . Holling⁶ first proposed that constraints on space use by animals could explain why home range should scale isometrically ($b = 1$): fractal habitat structure implies that smaller species exploit finer-grained features of the habitat than larger species and thus detect more resources. However, this theory did not explicitly address the issue of resource density and distribution. Most recently, Kelt and VanVuren¹⁸ proposed that home range does not exhibit a simple scaling relationship with size, as it changes nonlinearly according to size-dependent physiological constraints on animal's reproductive output and resource use. However, none of these hypotheses accounted for observed variation in exponents among trophic groups (for example, herbivores and carnivores¹⁵) and taxa (for example, birds and mammals^{12,13}). Thus, the evidence and theoretical explanations for a universal home range scaling law remain weak.

Here, we propose a new model to predict home range scaling with body size as a function of the spatial distribution and abundance of resources. This model provides the first theoretical synthetic explanation for why and how resource density scales with body size and the influence of resource density and distribution on home range scaling exponents. To survive, an individual must meet or exceed the energy it expends during maintenance, foraging, and reproduction B with resources gathered from the environment I such that $B \leq I$. To obtain resources, a forager instantaneously searches a volume of length w and dimension D as determined by whether its habitat is two- or three-dimensional. In two dimensions, for example, a forager would instantaneously search a square area with sides of length w . Over some time period t the forager samples v volumes per unit time, so the total volume $V(t)$ sampled over time t is tvw^D (refs 20, 21). An individual's home range results from movements over long time periods, for example, the resource renewal interval τ , or time required for a consumed resource to be renewed. Recent work²² shows that if τ is large then as $t \rightarrow \tau$, a random movement path will occupy a bounded volume, similar to a home range, H . Thus, as $t \rightarrow \tau$, $V(\tau) \approx H$.

Mounting evidence suggests that resource distributions are typically fractal-like: they exhibit statistically similar patterns over 2–3 orders of magnitude in scale of observation^{1,21,23,24}. A fractal resource distribution makes resource density scale dependent: different-sized species encounter different densities of resources in the same environment^{20,21}. To see this, consider that a forager maximizing its resource intake rate should minimize the number of sampling volumes needed for it to consume all resources in a landscape (Fig. 1). The resulting minimum number of sampling volumes will be spatially arranged to yield the maximum average

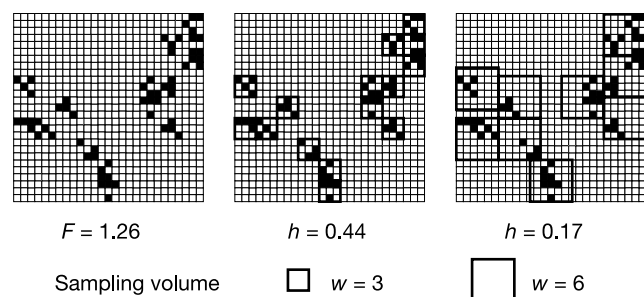


Figure 1 Hypothetical average density h of resources per sampling volume encountered by species with different sampling volumes of length w on a fractal distribution of resources (black cells, fractal dimension $F = 1.26$). The resource distribution was generated using random "Sierpinski gaskets"²⁵. Note that the species with the larger sampling volume encounters a lower average density of resources per sampling volume but requires fewer sampling volumes to incorporate all resources.

amount of resource per sampling volume^{1,23}. If so, the amount of resource per sampling volume will be, on average, $c_1 w^F$ (refs 1, 20, 21). The fractal dimension F describes the degree to which resources fill space and can range from 0, a single point, to 3, a solid cube^{1,20,21,25}. The constant c_1 describes resource density in the vicinity of other resources (clumping) as well as overall resource density^{1,20,21,25}. In general, both c_1 and F will increase as resource density increases (Fig. 2), but each can assume a range of values at most resource densities, depending on the spatial arrangement, and aggregation of the distribution²⁶. This property has a profound effect on the relationship of resource encounter rate with body size, and thus home range scaling: changes in resource density affect both the prefactor C_1 and the scaling exponents describing these relationships.

This scale-dependence of resource amount per sampling volume constrains the maximum resource density encountered by different sized foragers and thus total resource intake I and home range size (Fig. 1). Resource density r is the average amount of resources in a sampling volume $c_1 w^F$ divided by the sampling volume w^D , so $r = c_1 w^F / w^D = c_1 w^{F-D}$. Because F cannot exceed the dimension of the foraging habitat D over the same range of scales^{20,21}, $F \leq D$ and r must decline with increasing foraging scale w (refs 20, 27). Resource availability within the home range I within the resource renewal interval τ is the product of the home range H and r . Hence:

$$I = H c_1 w^{F-D} \quad (2)$$

This resource availability must be large enough to satisfy metabolic requirements B and this constrains the home range size to be at least:

$$H \geq \frac{B}{c_1 w^{F-D}} \quad (3)$$

This formula explicitly includes the effect of foraging scale on encountered resource abundance and thus home range.

To predict home range scaling relationships with body size, we can substitute well-known allometric functions for resource requirements: $B = c_2 M^{3/4}$ (refs 2–4), where c_2 is a taxon-specific

constant that includes species-specific resource demands over the resource renewal interval τ . We can also assume that the width of the search volume w is proportional to a physical distance, such as the forager's stride length³, which scales as $c_3 M^{1/3}$. These assumptions yield:

$$H = k M^{3/4 + D/3 - F/3} \quad (4)$$

where the prefactor $k = c_2 c_3^{D-F} / c_1$. The model predicts that there should not be a universal scaling exponent for home range size. The scaling exponent b is instead a function of the structure of the environment, as given by the dimension D , and the resource distribution as given by the dimension F . The exponent reflects the interaction between 1/4 power scaling of organism physiological rates, the structure of the environment, and the euclidean 1/3 power scaling of physical distances. The model predicts that, when $D = 2$, b will range from 3/4 when $F = 2$ to 17/12 as $F \rightarrow 0$. When $D = 3$, b will approach 21/12 as $F \rightarrow 0$. As expected if the minimum scale of resolution, $w = 1$, the coefficient k will increase with resource requirements (c_2) and movement rate (c_3) and decrease with greater resource density and/or clustering (c_1). Thus, for a given body mass, home range can vary widely depending on environmental con-

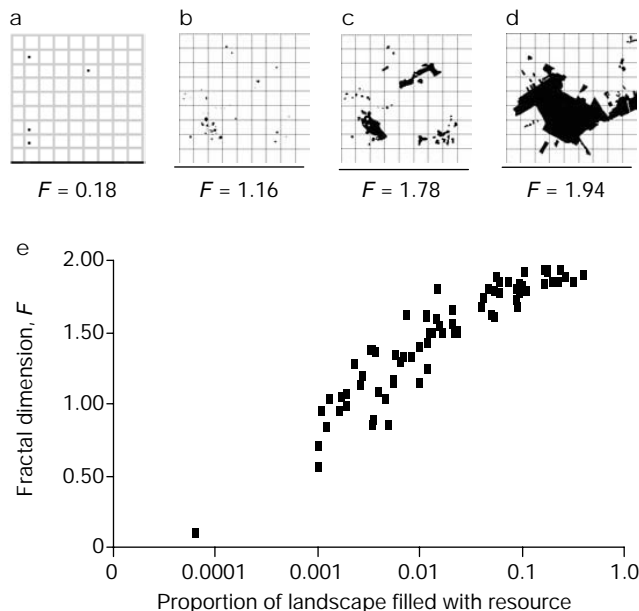


Figure 2 Relationship between density and estimated fractal dimension for different distributions in a two-dimensional environment. We illustrate this with real maps of some fractal distributions²⁶ of varying density, along a gradient of proportion of map filled (e). Although the fractal dimension varies at a given resource density, it increases with increasing density from almost 0 to 2 (a to d) over four orders of magnitude of proportional fill.

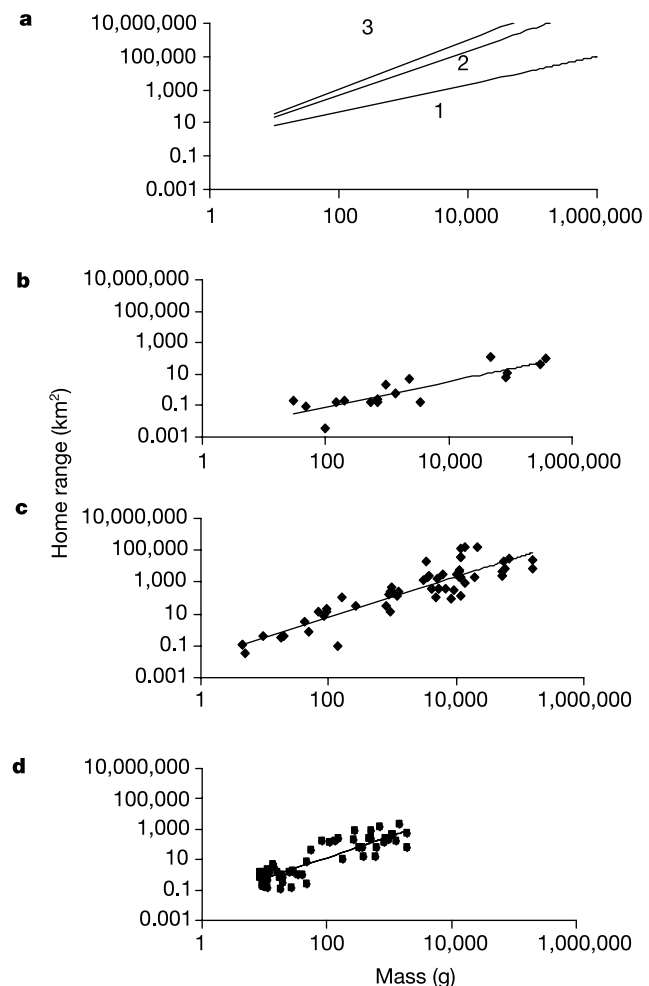


Figure 3 Comparison of model predictions and empirical estimates for home range–body mass scaling relationships (see also Table 1). **a**, Predicted scaling exponents b by trophic level: (1) terrestrial mammalian herbivores ($b \approx 5/6$); (2) terrestrial mammalian carnivores ($b \approx 4/3$); (3) terrestrial avian carnivores ($b \approx 3/2$). **b**, **c**, **d**, Observed relationships for terrestrial mammalian herbivores (**b**; $b \approx 0.83$, $R^2 = 0.74$) and terrestrial mammalian carnivores (**c**; $b \approx 1.21$, $R^2 = 0.80$) and terrestrial avian carnivores (**d**; $b \approx 1.37$, $R^2 = 0.78$; see Table 1).

Table 1 Predicted and observed home range scaling parameters

Foraging guild	Food resource	Expected F -values	Predicted b	Decimal equivalent	Observed b	s.e.	Observed Y_0	s.e.	N
Folivorous mammals*	Plant leaves	1.5–1.99	3/4–11/12	0.75–0.91	0.831	0.21	NA	NA	21
Folivorous mammals†	Plant leaves	1.5–1.99	3/4–11/12	0.75–0.91	0.802	0.11	0.0021	0.0003	16
Carnivorous mammals	Small vertebrates	0.5–1	15/12–17/12	1.08–1.25	1.213	0.11	0.0234	0.0053	32
Carnivorous birds	Small animals	0.5–1	17/12–19/12	1.41–1.58	1.374	0.09	0.0257	0.0031	58

Predicted home range scaling exponents (b) and coefficients (Y_0) compared to observed values from relationships of home range (km^2) versus body mass (in g) for herbivorous and carnivorous terrestrial mammals and carnivorous terrestrial birds^{5,6,9,13,15,28,29,30}.

*Regression results from Owen-Smith¹⁶; NA, individual data not available. Group home range divided by group size to estimate the area used by an individual.

†Home range divided by density to estimate the area used by an individual⁹.

Carnivorous mammals are non-social carnivores^{6,9,13,15}. Carnivorous birds are insectivorous and flesh-eating birds^{5,28,29}.

ditions, locomotory capacity and resource density.

Home range–body size relationships for carnivorous and herbivorous mammals and carnivorous birds strongly support the predictions of the model. Data from published sources^{5,6,9,13,15,28,29} were combined into one data set and an average mass and home range was recalculated for each species (see Methods). We estimated the range of likely fractal dimensions for plant leaves^{1,21} and for the prey of carnivores from published sources and data from Portal, Arizona³⁰. As demonstrated in Fig. 2, F varies predictably with resource density. Low-density resources in two dimensions such as small mammal prey should have F -values ranging from near 0 to 0.5. In three dimensions, small animal prey such as insects and small vertebrates should have F -values ranging from 0.5 to 1. Relatively high-density resources such as plant leaves should have F -values between 1.5 and 2. In our model, these estimates suggest that b for mammals feeding in a two-dimensional environment should range from 3/4 to 11/12 for herbivores, and from 13/12 to 15/12 for carnivores. Furthermore b should range from 17/12 to 19/12 for carnivorous birds feeding in three-dimensional environments. As shown in Table 1, these predictions correspond closely with the results of our analyses (Fig. 3).

The model has profound implications for ecologists and wildlife managers because it shows how resource spatial distribution, and thus habitat fragmentation, might affect home range. Home range scaling exponents larger than 3/4 suggest that larger species use much larger areas than would be expected on the basis of their resource requirements. Furthermore, habitat fragmentation that results in a loss of resource density and thus lower c_1 and F may greatly increase home range size, and this increase will be much greater for larger species. In a two-dimensional environment ($D = 2$), for example, the sensitivity of predicted home range size H (equation (4)) to changes in c_1 is $\partial H / \partial c_1 = -c_2 c_3^{-2-F} M^{17/12-F/3} / c_1^2$. This result implies that a decrease in c_1 will increase H and the increase will be greater for larger species, because $\partial H / \partial c_1$ is proportional to M . Likewise, the sensitivity of home range size to changes in the resource fractal dimension F is $\partial H / \partial F = -[\ln(c_1) + (1/3)\ln(M)]c_2 c_3^{-2-F} M^{17/12-F/3} / c_1$. This result implies that a decrease in F will also increase H and do so more strongly for larger species. Thus, habitat loss will require greater compensatory changes in home ranges of larger species, and lead to a steeper body size scaling relationship for home range. These predictions emphasize the high potential vulnerability of large carnivores to habitat fragmentation. Carnivores have naturally low-density prey, and thus low c_1 and F -values, and therefore little ability to compensate for reductions in c_1 and F . In contrast, herbivore species, whose plant resources tend to occur at much higher density and thus fractal dimension, can potentially expand their home ranges by 2–3 orders of magnitude to compensate for habitat fragmentation.

Our home range model, based on an assumption of fractal resource distributions, predicts that there is no universal scaling law for home range. Instead, the range of variation in scaling exponents, b , is constrained between a minimum of 3/4 and a maximum of 17/12 for organisms in two-dimensional environments, and a maximum of 21/12 in three-dimensional environ-

ments. The model unifies previous hypotheses of home range scaling by incorporating two fundamental properties of fractal-like environments: (1) the relationship between resource distribution F and resource density r (Fig. 2); and (2) the decline in resource density with increasing foraging scale w (Fig. 1). These properties provide a potential framework for understanding scaling relationships for other interactions between individuals and their environment^{20,21,23}. Here we have generated a framework for exploring important sources of variation in home range scaling. These include differences in scaling exponents among different trophic and taxonomic groups and the effects of habitat fragmentation. Clearly, there are many factors besides body size that influence home range size, such as population density, temperature and other factors that influence resource demand, that we have not included explicitly in our model. However, it seems unlikely that these factors would affect the body size scaling exponents for home range. The agreement of the scaling exponents predicted by our model with exponents of observed relationships suggests that resource distribution and density are critical factors affecting home range scaling relationships. □

Methods

Home range data for bird and mammal species were taken from published sources^{5,6,9,13,15,28,29}. In our analysis, we only included those species (1) for which we unambiguously knew the type of food resources, and (2) from diet guilds for which we could estimate ranges of fractal dimensions of resource distribution. Data for individual species were averaged to obtain a single home range (in km^2) and body mass (in g) value for each species. Data was log transformed and least squares regression was used to estimate the observed home range scaling exponent.

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Competing interests statement

The authors declare that they have no competing financial interests.

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The endogenous cannabinoid system controls extinction of aversive memories

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Acquisition and storage of aversive memories is one of the basic principles of central nervous systems throughout the animal kingdom¹. In the absence of reinforcement, the resulting behavioural response will gradually diminish to be finally extinct. Despite the importance of extinction², its cellular mechanisms are largely unknown. The cannabinoid receptor 1 (CB1)³ and endocannabinoids⁴ are present in memory-related brain areas^{5,6} and modulate memory^{7,8}. Here we show that the endogenous cannabinoid system has a central function in extinction of aversive memories. CB1-deficient mice showed strongly impaired short-term and long-term extinction in auditory fear-conditioning tests, with unaffected memory acquisition and consolidation.

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Treatment of wild-type mice with the CB1 antagonist SR141716A mimicked the phenotype of CB1-deficient mice, revealing that CB1 is required at the moment of memory extinction. Consistently, tone presentation during extinction trials resulted in elevated levels of endocannabinoids in the basolateral amygdala complex, a region known to control extinction of aversive memories⁹. In the basolateral amygdala, endocannabinoids and CB1 were crucially involved in long-term depression of GABA (γ -aminobutyric acid)-mediated inhibitory currents. We propose that endocannabinoids facilitate extinction of aversive memories through their selective inhibitory effects on local inhibitory networks in the amygdala.

To study the involvement of the endogenous cannabinoid system in memory processing, we generated CB1-deficient mice (CB1^{-/-}; see Supplementary Information). CB1^{-/-} mice and CB1^{+/+} littermates were tested in auditory fear conditioning, which is highly dependent on the amygdala¹ and enables the dissection of different phases of memory formation, including acquisition, consolidation and extinction. Mice were trained to associate a tone with a foot-shock (conditioning). After conditioning, animals froze when

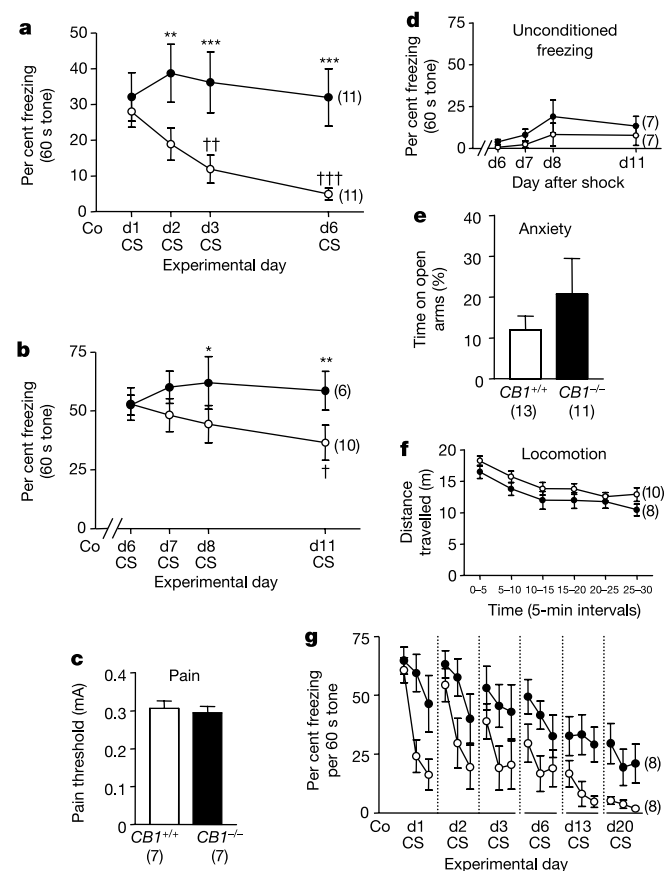


Figure 1 Impaired extinction of aversive memory in an auditory fear-conditioning task of CB1^{-/-} mice (filled circles) as compared to their CB1^{+/+} littermates (open circles). **a, b**, After conditioning (Co) animals were repeatedly exposed to 60 s tones (conditioned stimulus, CS) starting 24 h after conditioning (**a**) (d1) or after a 6-day consolidation period (**b**) (d6). **c–f**, CB1^{-/-} and CB1^{+/+} mice did not differ in their sensory-motor abilities, as assessed by sensitivity to rising electric foot-shock (**c**), unspecific freezing to a tone after shock application (**d**), anxiety-related behaviour on the elevated plus maze (**e**) and horizontal locomotion in an open field (**f**). **g**, CB1^{-/-} mice showed memory extinction in response to a stronger extinction protocol (3 min tones until day 20; analysed in 60-s intervals), but still froze more than CB1^{+/+} controls. Means \pm s.e.m. are shown; number of animals are indicated in parentheses. Asterisk, $P < 0.05$; double asterisk, $P < 0.01$; triple asterisk, $P < 0.001$ (compared with CB1^{+/+}); dagger, $P < 0.05$; double dagger, $P < 0.01$; triple dagger, $P < 0.001$ (compared with day 1).